

Under the scales: Identification of ticks in rehabilitated African pangolins and confiscated scales

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ABSTRACT

Pangolins are the most trafficked mammals globally. Beyond zoonotic concerns related to coronavirus, pangolins serve as hosts for ectoparasites such as ticks, which can be inadvertently transported through illegal wildlife trade and rehabilitation efforts. The transcontinental trafficking of pangolins and their derivatives poses a potential risk of pathogen spillover affecting humans, wildlife, and livestock. Despite these concerns, data on tick infestations in confiscated African pangolins and scales remain scarce. This study aims to identify tick species associated with confiscated pangolins and scales using morphological and molecular approaches. A total of 275 ticks were collected from 17 rehabilitated African pangolins (*Smutsia temminckii*, *Phataginus tricuspis*, *Phataginus tetradactylus*) and nine bags of seized scales. Representative specimens ($n = 53$) were genetically analyzed by amplifying the 16S rRNA fragment and comparing sequences with publicly available data. Morphological identification revealed five tick species: *Amblyomma compressum*, *A. hebraeum*, *Ornithodoros compactus*, *Rhipicephalus theileri*, and *R. simus*. Taxonomic assignments conformed with the DNA-based identification for all species except for '*O. compactus*' which resulted in *O. moubata*. These discrepancies may be due to overlapping morphological characters between the two *Ornithodoros* species. Notably, ticks from the three identified genera are known vectors of pathogens causing diseases such as heartwater, anaplasmosis, babesiosis, theileriosis, African swine fever, and human relapsing fever. We provide the first record of *A. hebraeum* in *Phataginus* species, and *A. compressum* in *P. tetradactyla*, expanding their host range. This study also establishes a baseline for tick diversity in confiscated African pangolins and scales trafficked within Africa and out of Africa. The findings highlight the importance of integrative taxonomic approaches in tick identification and emphasize the need for further research incorporating additional genetic markers and morphometric analyses to enhance species resolution.

1. Introduction

Family Manidae (pangolin) comprises nine extant species, with five occurring exclusively in Asia and the other four restricted to the African continent. (Gu et al., 2023; Hu et al., 2020; Zhang et al., 2022). Pangolins are currently considered the most trafficked wild mammals globally, with estimates indicating that over one million individuals have been traded since the year 2000 (Emogor et al., 2021; Heinrich et al., 2017; Ingram et al., 2018; Omifolaji et al., 2020). This escalating

illegal trade is driven by increasing demand for pangolin products, particularly their meat, skins, and scales which are used in traditional medicine and consumed as delicacies in both Africa and Asia (Boakye et al., 2015; Ingram et al., 2022; Malimbo et al., 2020; Nguyen et al., 2021; Nijman, 2023; UNODC, 2016). The increased demand in Asian markets (Ingram et al., 2019; Svensson et al., 2013) has contributed to population declines among Asian pangolin species. As a result, thousands of African pangolins and their derivatives (e.g., scales and meat) are being confiscated between Africa and Asia in the process of meeting

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demand in Asian markets (Challender and Hywood, 2012; Emogor et al., 2021; Heinrich et al., 2016; Heinrich et al., 2017; Ingram et al., 2019; Svensson et al., 2013).

Reports from organizations involved in confiscations, social media pages, previous studies, and media news have identified countries such as Nigeria, DRC, Uganda, and Cameroon as major exporters and transits, while China, Singapore, and Vietnam are major importers and transits of African pangolins and scales (Emogor et al., 2021; Ingram et al., 2019; Nethavhani et al., 2025; Omifolaji et al., 2020). Although a decline in reported seizures was observed in 2019 (Emogor et al., 2021; Ingram et al., 2019; Nethavhani et al., 2025; Omifolaji et al., 2020), trade remains active, particularly in countries such as Nigeria and Vietnam (Nethavhani et al., 2025). One proposed explanation for the decline in illegal trade of pangolins and their derivatives may be heightened awareness of zoonotic risks following the COVID-19 pandemic, as pangolins and other animals such as bats were considered as potential hosts of zoonotic pathogens like SC2r-CoVs, Ebola, and HKU4-CoV (Cui et al., 2023; Li et al., 2024; Peng et al., 2021) transmitted between wild, domestic animals and human, leading to temporary trade restrictions.

Beyond zoonotic concerns related to COVID-19, pangolins are also potential hosts for ectoparasites such as ticks (Mohapatra et al., 2016), which may be inadvertently transported through the trafficking of pangolin derivatives and rehabilitation efforts. Ticks (Argasid and ixodid) serve as pathogen vectors such as viruses, helminth protozoans, and bacteria that cause tick-borne diseases such as heatwater, babesiosis, theileriosis, and anaplasmosis to humans, wildlife, and livestock (Aziz et al., 2025; Intirach et al., 2024; Jongejan and Uilenberg, 2004; Makwarela et al., 2024; Ngnindji-Youdje et al., 2022). Therefore, transcontinental movement of pangolins and their scales may pose a risk of pathogen spillover, which may be threatening to humans, wildlife, and livestock. For example, the movement of livestock and trade by humans has resulted in ticks and tick-borne diseases between and within continents (Aziz et al., 2025; Guglielmone and Robbins, 2018; Jongejan and Uilenberg, 2004; Motta et al., 2017). In pangolins, heavy tick infestations coupled with stress and injuries may also contribute to morbidity and mortality of rehabilitated individuals retrieved from confiscations (Li et al., 2024; Mohapatra et al., 2020). Similar to livestock, heavy tick infestation leads to blood loss, reduced milk production, weight loss, paralysis, and sometimes death (Makwarela et al., 2024; Schnittger et al., 2012), and this may extend to a wide range of hosts.

Despite the health risks, there is limited studies on the identification of tick species and tick-borne diseases in confiscated African pangolins and scales. Previous studies were limited to Asian countries and Asian pangolin species (Hassan et al., 2013; Khatri-Chhetri et al., 2016; Li et al., 2024; Mohapatra et al., 2020; Zhai et al., 2021). This study therefore, aims to identify tick species associated with rehabilitated African pangolins and confiscated scales using morphology and molecular identification methods.

2. Materials and methods

2.1. Ethical clearance

Ethical approval was obtained from the Ethics and Scientific Committee of the National Zoological Gardens (project P15/08)

2.2. Specimen collection

Live African pangolins were confiscated by law enforcement officials in South Africa (SA), Zimbabwe (Zim), and the Central African Republic (CAR). These pangolins were then taken to rehabilitation centers in the three African countries mentioned above. A total of 140 tick specimens were collected from under the scales of 17 live pangolins by staff members during rehabilitation assessments, which entails weighing the pangolins and checking for wounds or trauma. The ticks were

opportunistically removed using forceps from 14 live *Smutsia temminckii* (n = 130 ticks), two live *Phataginus tricuspis* (n = 7), and one live *Phataginus tetradactylus* (n = 3). In addition to the dataset, we received nine bags of African pangolin scales with unknown African origins that were confiscated by the Chinese Customs Authorities from Chinese ports. These scales were identified as belonging to three African pangolin species including *S. temminckii*, *P. tricuspis*, and *P. tetradactylus*. From the nine bags, a total of 135 tick specimens were collected: 74 ticks from *S. temminckii* scales, 34 from *P. tricuspis*, and 27 from a mixture of *P. tetradactylus* and *P. tricuspis* (Table S1).

2.3. Morphological identification of live pangolins, pangolin scales, and ticks

Live pangolins were identified by Prof. Raymond Jansen (Global expert on pangolin identification, Tshwane University of Technology), using the USAID draft identification guide by Cota-Larson (2017). Similarly, all scales in the bags were grouped according to their similarities and identified by Prof. Raymond Jansen, using the USAID guide. The African pangolins were identified as *S. temminckii*, *P. tricuspis*, and *P. tetradactylus*, and all scales belonged to these three species.

All nymph and adult tick specimens were identified morphologically to genus and species level where possible by Dr Heloise Heyne (Curator at The Gertrud Theiler Tick Museum, Pretoria, South Africa) using different taxonomic keys (Bedford and Hewitt, 1925; Uilenberg et al., 2013; Voltzit and Keirans, 2003; Walker et al., 2000; Walton, 1962; Zumpt, 1961), under a Zeiss V-20 stereo-microscope with through-focus software (Z-stacking). Tick specimens were grouped based on similar characters and categorized into three genera: *Amblyomma*, *Rhipicephalus*, and *Ornithodoros* (Fig. 1a–d), and subsequently stored in 70 % ethanol at –80 °C until further use (see Fig. 1).

2.4. DNA extraction, PCR amplification, and sequencing

DNA was extracted from 53 selected individual specimens by cross-sectional cutting (bilateral symmetry) and physical disruption of the tick exoskeleton, using the Epicentre MasterPure™ DNA Purification Kit according to the manufacturer's protocol. The extracted DNA was stored at –20 °C until use. The 16S rRNA and COI fragments were amplified using 16S + 1/16S-1 (Black and Piesmant, 1994) and universal LCO1490/HCO2198 (Hebert et al., 2003) primer pairs. Each final reaction volume of 25 µl contains 12 µl of DreamTaq Mastermix (Thermo Fisher Scientific Inc.), 1 µl of DNA template, 1 µl of each primer, and 11 µl of nuclease-free water. The PCR cycling conditions were as follows: initial denaturation at 94 °C for 5 min; 5 cycles of 94 °C for 15 s, 51 °C for 30 s, 68 °C for 30 s; 25 cycles 94 °C for 15 s, 51 °C for 30 s, 68 °C for 30 s; 72 °C for 1 min and a final extension at 70 °C for 5 min. PCR products were sequenced unidirectionally with the 16S-1 primer, using the Applied Biosystems BigDye Terminator v3.1 Cycle Sequencing Kit following the manufacturer's protocol. Novel DNA sequences were deposited on GenBank under accession numbers PV458289 – PV458341.

2.4.1. DNA sequence analyses

Novel sequences were queried against the GenBank (<https://blast.ncbi.nlm.nih.gov/>) to confirm species identification. Genetic clustering were conducted for three genera (*Amblyomma*, *Rhipicephalus* and *Ornithodoros*) (Fig. 1a–d) using novel sequences and public sequences filtered to; (a) sequences that yielded identification similarities of ≥90 % in BLAST, (b) strictly 16S rRNA gene, (c) sequences identified to species level, (d) species that are represented by more than one sequence, and (e) sequences longer than 350 bp. Final three datasets included: (a) eight novel sequences and 28 sequences of genus *Amblyomma* retrieved from GenBank representing 11 species, (b) seven novel sequences and 24 sequences of genus *Rhipicephalus* from GenBank, and (c) 38 novel sequences and 14 sequences of genus *Ornithodoros* from GenBank representing five species (Table S2). Morphological verifications of the

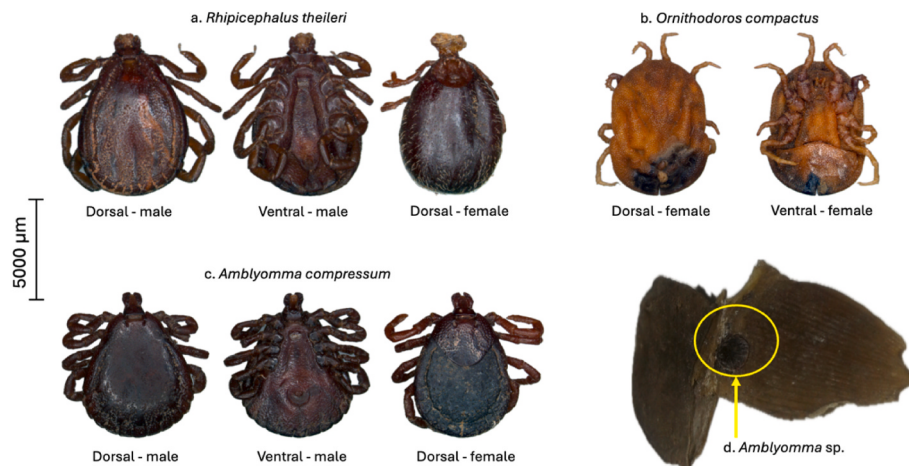


Fig. 1. Tick specimens from three genera: a. *Rhipicephalus*, b. *Ornithodoros*, and c-d. *Amblyomma* recovered from live African pangolins and scales, © Heloise Heyne.

sequences acquired from GenBank were done in their respective published studies (Bakkes et al., 2018, 2021; Monakale et al., 2024; Ngoy et al., 2021a; Scoles, 2004). Multiple alignments were generated using the MAFFT algorithm in Geneious Prime v.2025.0.3 (<https://www.geneious.com>). Genetic clustering was accessed using a maximum likelihood (ML) tree generated on the IQ-TREE online server (<https://www.iqtree.org>), under best models: TIM + F + I + G4, TPM3+F + G4, and TPM2+F + I + G4 for genera *Amblyomma*, *Rhipicephalus*, and *Ornithodoros* respectively, according to the BIC. Branch supports were determined using 1000 replicates for both the ultrafast bootstrapping (UFBoot) and the SH-aLRT branch test (Guindon et al., 2010; Hoang et al., 2018). The visualization of all trees was done in FigTree v1.4.4 (<http://tree.bio.ed.ac.uk/>). Intraspecific maximum p-distances (maximum p-distance,%) were calculated in MEGA X, under the K2P model. A commonly accepted threshold for species-level divergence based on 16S rRNA sequences is 5 %, with interspecific distances typically exceeding this value (Lv et al., 2014a, 2014b; Pagueu et al., 2023).

3. Results

3.1. Morphological identification of ticks

3.1.1. Ticks on rehabilitated pangolins in CAR and the Northern Cape of South Africa

A limited number of specimens were intact for photography, as such, images for *A. hebraeum* and *R. simus* could not be presented. Despite the nature and quality of some specimens that were not intact, a total of 140 ticks from *S. temminckii*, *P. tricuspis*, and *P. tetradactyla* were identified to species level. A large proportion (93 %) of ticks were found in *S. temminckii* and identified as *Ornithodoros compactus* (n = 116) and *Rhipicephalus theileri* (n = 14), followed by ticks found in *P. tricuspis* (5 %) identified as *Amblyomma compressum* (n = 7), and those found in *P. tetradactyla* (2 %) also identified as *A. compressum* (n = 3) (Fig. 2a).

3.1.2. Ticks on confiscated African pangolin scales from an unknown origin

All 135 ticks found were identified, with 55 % of ticks from *S. temminckii* scales identified as *A. compressum* (n = 74). All ticks from *P. tricuspis* (25 %) scales were also identified as *A. compressum* (n = 34), while ticks (20 %) from a bag with mixed scales of *P. tricuspis* and *P. tetradactyla* were identified as *A. compressum* (n = 23), *A. hebraeum* (n = 2), and *R. simus* (n = 2) (Fig. 2b).

3.1.3. Morphological characterization of ticks from African pangolins in rehabilitation and confiscated scales

Species in the genus *Amblyomma* are characterized by a long hypostome, elongated palps, large flat eyes, and an ornamented scutum present in females or conscutum in males, consistent with descriptions by Jongejan and Uilenberg (2004) and Walker et al. (2003). *Amblyomma hebraeum* is distinguished by a dark brown ground colour, with pale yellow ornamentation tinged coppery-green at the edges, festoons, and an anal plate in males (Walker et al., 2003).

Genus *Rhipicephalus* is characterized by short mouthparts, eyes, and festoons, a distinct anal groove, spiracular plates with a tail-like protrusion, and a basis capitula hexagonal dorsally, with males exhibiting ventral plates (Walker et al., 2000). *Rhipicephalus simus* showed a large, dark, smooth scutum with punctations delineating the cervical groove in females and four longitudinal rows of punctations in males, aligning with identifications in Makwarela et al. (2024).

Rhipicephalus theileri is a small, broad, yellowish to reddish-brown tick. Both sexes have short, broad palps (Walker et al., 2000). Males have a conscutum with a small anterior process on coxae I, convergent cervical pits, and a distinct pseudoscutum with minimal punctations. Punctations increase in size and density posteriorly. Females have a broader scutum with scattered punctations, particularly on the scapulae and cervical fields, but it remains smooth and shiny. The alloscutum bears broad longitudinal bands of white setae.

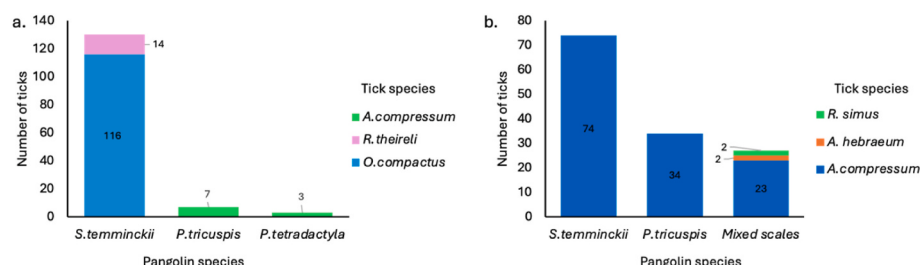


Fig. 2. Number of ticks identified morphologically from African pangolins sent for (a) rehabilitation and (b) confiscated scales.

3.2. Genetic identification of ticks on rehabilitated pangolins and confiscated pangolin scales

Since there was no amplification for the COI fragment for all specimens, we therefore proceeded with the analyses of 16S rRNA. The PCR amplification for the 16S rRNA (~415 bp) fragment was successful for 53 representative specimens identified as from genera *Amblyomma*, *Rhipicephalus*, and *Ornithodoros* based on the >90 % threshold BLAST results (Table 1).

3.2.1. Genus *Amblyomma*

Novel sequence PARA 148 identified as ‘*A. hebraeum*’ resulted in 100 % similarity and clustered with reference sequences of *A. hebraeum* (PQ000334) from South Africa (Table 1) (Monakale et al., 2024) with high nodal support (Fig. 3a). The maximum p-distance in this cluster was 0.00 %, indicating conspecificity and accurate identification of the novel sequence as *A. hebraeum*. Furthermore, the remaining six novel sequences of specimens morphologically identified as ‘*A. compressum*’ resulted in 94.6 %–96.9 % similarity and clustered with sequences of *A. compressum* (MN032119) from the Democratic Republic of the Congo (DRC) (Table 1) (Ngoy et al., 2021a) with high nodal support (Fig. 3a). The maximum p-distance ranged between 2.00 % and 16.00 %. The high maximum p-distance may represent cryptic diversity or more than one species. However, we cannot rule out the possibility of phylogeographic structure where these sequences may belong to the same species (*A. compressum*), which originated from different geographical locations.

3.2.2. Genus *Rhipicephalus*

For specimens (PARA08, 11A-D, and 14) morphologically identified as ‘*R. theileri*’ (maximum p-distance = 0.00 %–5.00 %), no reference sequences for this species were available prior to this study. However, the divergence between other sequences ranges between 0.00 % and 1.00 % when excluding PARA 5, which may suggest a separate species or phylogeographical structure. These novel sequences are somewhat similar to those of *R. turanicus*, *R. sanguineus*, *R. haemaphysaloides* and *R. simus* with 90.0 %–90.6 % in BLAST results (Table 1) cluster separately and as sister cluster to those of species on the ML tree, signifying they are different species but closely related (Fig. 3b). The novel sequence ‘PARA 150’ resulted in 95.98 % similarity to *Rhipicephalus simus* (MW080137) from South Africa (Bakkes et al., 2021), and clusters with reference sequences of *R. simus* from South Africa with high nodal support (Table 1; Fig. 3b). The maximum p-distance of the reference sequences ranged from 0.00 % to 1.00 %, and increased to a range between 11.00 % and 14.00 % when adding the novel sequence PARA 150,

indicating the presence of more than one species or phylogeographical structure.

3.2.3. Genus *Ornithodoros*

All specimens identified as ‘*O. campactus*’ had between 98.3 % and 99.8 % similarities with *O. moubata* (MF415628) from South Africa (Bakkes et al., 2018), *O. moubata* (LC492106) from Zambia, and *O. pornicus* (AY375443) from Southern Africa (Scoles, 2004) (Table 1). Furthermore, the novel sequences clustered with reference sequences of *O. moubata/pornicus* with high nodal support (0.00 %–4.00 %), suggesting conspecificity with reference (Fig. 4). However, there is a great variation between novel sequences without reference sequences, with divergent between most sequences between ranging between 3.00 % and 9.00 %.

4. Discussion

Accurate tick identification is crucial for effective zoonotic disease surveillance and management (Aziz et al., 2025; Lv et al., 2014a, 2014b; Makwarela et al., 2024). While morphological identification of ticks has been widely used, it is often unreliable and inadequate when specimens are damaged, have limited characters to distinguish closely related species, engorged or immature specimens (Aziz et al., 2025; Diarra et al., 2017; Kammah and El-Fiky, 2005; Walker et al., 2003). Studies on tick identification are currently using additional identification methods such as molecular taxonomy (i.e., COI, 12S rRNA, ITS-2, 18S rRNA, and 16S rRNA) (Aziz et al., 2025; Coimbra-Dores et al., 2018; Kammah and El-Fiky, 2005; Khatri-Chhetri et al., 2016; Lv et al., 2014a, 2014b; Makwarela et al., 2024), MALDI-TOF mass spectrometry (Diarra et al., 2017; Ngoy et al., 2021b), and morphometrics (Bakkes et al., 2018) to complement classic taxonomy. Our study used morphology and molecular (16S rRNA) tools to identify ticks found on confiscated African pangolins and scales.

None of the specimens yielded amplification of the COI fragment using universal primer pairs, whereas 100 % successfully amplified the 16S rRNA fragment. Albeit successful amplification of the COI fragment using universal primers for tick species such as *Rhipicephalus appendiculatus* (Amzati et al., 2018), the failure to amplify the COI fragment in ticks with the universal primers in our study is consistent with previous findings (Lv et al., 2014a) and may be attributed to high sequence variability at the primer binding sites. However, we cannot rule out the possibility of poor DNA quality resulting from specimen age, desiccation, and storage in 70 % ethanol which may have further contributed to the amplification failure. The successful amplification of the shorter 16S rRNA fragment supports the latter hypothesis, as shorter targets are more likely to amplify from degraded DNA. While the use of more species-specific or adjusted COI primers may improve amplification success (Lv et al., 2014a, 2014b), the degree of DNA degradation may still limit the efficacy. In such cases, designing primers that target shorter fragments which may be concatenated to produce a 710bp COI fragment may provide a more effective solution.

The integration of molecular and classical taxonomy was confirmed in all tick species identified (4/5, 80 %), except for genus *Ornithodoros* which was likely a case of taxonomical misclassification. Our study confirms the presence of *A. compressum*, *A. hebraeum*, *R. simus*, and *R. theileri*, and *O. moubata* in the confiscated African live pangolins and scales. *Amblyomma compressum* was recovered in *S. temminckii* scales and *P. tricuspis* (pangolins and scales), with a first record on *P. tetradactyla* pangolins and scales. Consistent with previous studies, *Amblyomma compressum* has been reported on *S. temminckii* from the DRC and Central Republic of Africa, and *P. tricuspis* from the CAR and Liberia (Mediannikov et al., 2012b; Mohapatra et al., 2016; Uilenberg et al., 2013). A recent study on ticks and *Rickettsia* associated with wild animals sold in markets in Cameroon reported *A. compressum* as the most common in *P. tricuspis* (Paguem et al., 2023). Interestingly, the presence of *A. compressum* in our study was only recovered in the scales of

Table 1
The BLASTn query results of tick species found in rehabilitated African pangolins and confiscated scales.

Sample ID	Morphology	Identity (%)	Reference sequences (Accession number)
PARA3A-B, Para4, 4–47, PARA5, PARA6C-M, PARA7, PARA9H-I, PARA12B-P, PARA23	<i>Ornithodoros compactus</i>	98.30–99.80	<i>Ornithodoros moubata</i> (MF415628, LC492106), <i>Ornithodoros pornicus</i> (AY375443)
PARA19, PARA21, PARA104, PARA110, PARA116, PARA120, PARA122	<i>Amblyomma compressum</i>	95.10–96.90	<i>Amblyomma compressum</i> (MN032119)
PARA148	<i>Amblyomma hebraeum</i>	100	<i>Amblyomma hebraeum</i> (PQ000334)
PARA150	<i>Rhipicephalus simus</i>	95.98	<i>Rhipicephalus simus</i> (MW080137)
PARA8, PARA11A-D	<i>Rhipicephalus theileri</i>	90.00–90.60	<i>Rhipicephalus</i> spp.

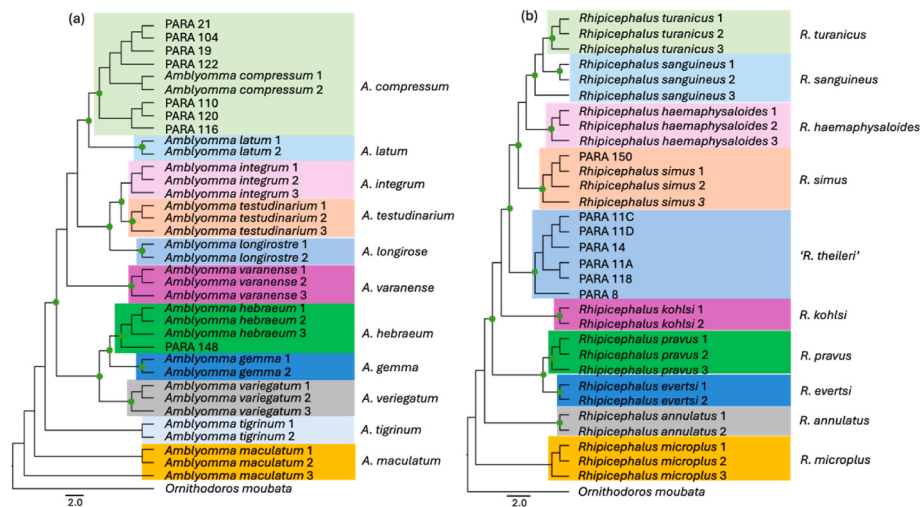


Fig. 3. Maximum-likelihood trees for genera (a) *Amblyomma* and (b) *Rhipicephalus*, based on new (PARA) and publicly available 16S rRNA sequences. The green circles represent nodal support values displayed only for UFBoot/SH-aLRT >90 %.

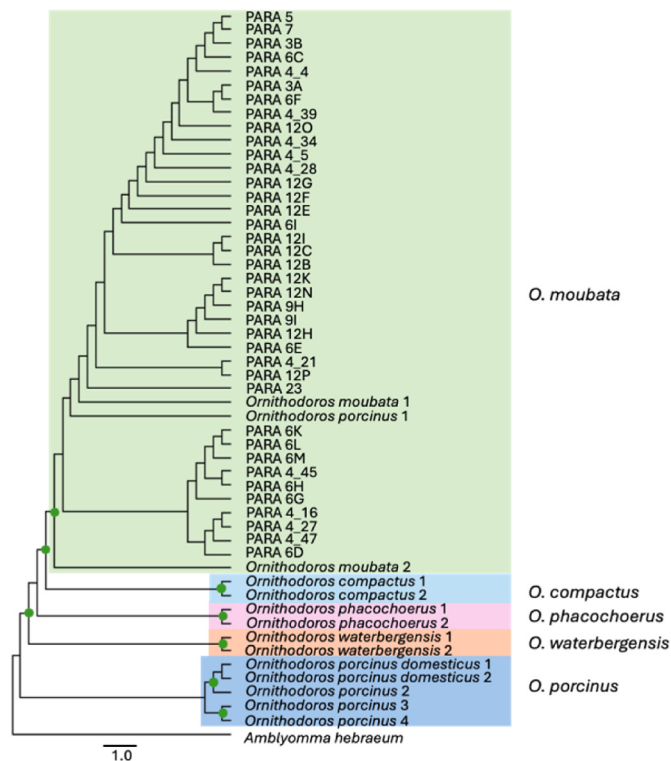


Fig. 4. Maximum-likelihood trees for genus *Ornithodoros*, based on new (PARA) and publicly available 16S rRNA sequences. The green circles represent nodal support values displayed only for UFBoot/SH-aLRT >90 %.

S. temminckii and not in live pangolins. Given the thorough identification of both pangolins and scales by an expert, it is possible that the confiscated live pangolins (*S. temminckii*) and scales originated from different locations with differing tick distributions. The first-time record of *A. compressum* in *P. tetradactyla* species may suggest either an expansion of the tick's known host range or possible contamination from *P. tricuspid* due to co-storage. *Amblyomma compressum* is a vector of *Rickettsia africae*, which causes African tick-bite fever, representing a potential zoonotic threat (Mediannikov et al., 2012a; Mohapatra et al., 2016; Paguem et al., 2023).

Amblyomma hebraeum is typically associated with large wild

ruminants and cattle (Horak et al., 2017; Makwalela et al., 2024; Walker et al., 2003), and has not been previously reported on host pangolins. This tick species is frequent in humans and is transported by humans, facilitating its spread across Africa and beyond (Guglielmone and Robbins, 2018). *Amblyomma hebraeum* transmits multiple pathogens including *Ehrlichia ruminantium*, which causes heartwater in livestock, *Rickettsia africae* and *R. conorii* causing tick-bite fever in humans, and *Theileria* mutants causing benign theileriosis in cattle (Horak et al., 2017; Jongejan et al., 2020; Walker et al., 2003). The finding of *A. hebraeum* on *Phataginus* pangolins may suggest either an emerging host-parasite relationship or an incidental host association, given that only two specimens were found. In either case, further research on the relationship of this parasite-host association is warranted given the potential health risks for both wildlife and human populations.

In our study, *R. simus* was found in a mixed bag of *Phataginus* species scales, consistent with a study that identified *R. simus* as one of the ectoparasites of *P. tricuspid* in Nigeria (Fawole et al., 2023). However, this species frequently infests humans, monogastric domestic and wild animals, and birds (Aziz et al., 2025; Makwalela et al., 2024; Walker et al., 2000). It is a known vector of *R. conorii*, causative of Mediterranean spotted fever in humans (Walker et al., 2000), *Babesia traubmanni* to pigs, *Theileria* sp., *Anaplasma* sp. to cattle, and tick paralysis to humans. Recently, *R. simus* has been identified as a possible new host for phleboviruses which are causative agents of severe fever in humans (Munjita et al., 2024), highlighting an urgent public health concern and the risk of transmission during pangolin scale trafficking. The presence of *R. simus* in trafficked pangolins may have implications for pathogen transmission. However, given that only two specimens were found, it is necessary to collect these ticks from wild pangolins to definitively term them a proper infection. Species *R. theileri* has been reported to be found on both domestic and wild animals, including Temminck's pangolins. This is consistent with our findings, despite being exclusive to *S. temminckii* live pangolins and not on the scales. Although *R. theileri* is not known to transmit pathogens (Walker et al., 2000), its presence in *Smutsia temminckii* in our study may warrant further investigation on potential health risks.

Molecular characterization of *O. compactus* revealed high sequence similarity to *O. moubata* reference sequences in the NCBI database, highlighting potential challenges in species delineation. Previous studies have reported difficulties in distinguishing *Ornithodoros* species based on morphology due to overlapping characters, particularly in the nymphal stage (Bakkes et al., 2018; Jori et al., 2023). While both species share similar body shape, *O. moubata* has bulbous posterior mammillae,

whereas *O. compactus* has flat, tile-like dorsal mammillae (Bakkes et al., 2018). In our study, identification was done during nymphal stage, which may have contributed to confusion, thus leading to common misidentification. Our phylogenetic analyses recovered *O. compactus* and *O. moubata* as sister taxa, consistent with findings from Bakkes et al. (2018) and Craig et al., 2022, supporting the monophyly of these species with high sequence similarity and high nodal support.

Apart from the morphological characteristics, their biogeographic distribution and host specificity may also aid in their identification. *Ornithodoros compactus* is typically found in the southwestern regions of South Africa, receiving less than 300 mm annual precipitation and primarily associated with tortoise (Bakkes et al., 2018; Jori et al., 2023). In contrast, *O. moubata* is more widespread in the northwestern regions of South Africa, with more than 400 mm annual precipitation, and has a broader host range, including *Smutsia pangolins* (Bakkes et al., 2018). The presence of the *Ornithodoros* ticks in *Smutsia temminckii* in our study supports the molecular identification as *O. moubata* rather than *O. compactus*. Given its role as a vector of *Borrelia duttoni* which causes human relapsing fever and a virus causing African swine fever, further research is needed to assess its zoonotic disease risk and transmission.

4.1. High intraspecific distances and phylogeographical structure within species

The commonly accepted threshold for species-level in ticks using the 16S rRNA fragment is approximately 5 %, and values exceeding this are typically indicative of distinct species (Lv et al., 2014a, 2014b; Paguem et al., 2023). In our study, however, the genetic divergence observed among some specimens classified as conspecifics exceeded this threshold. Notably, this pattern was apparent in sequences assigned to *R. simus*, *A. compressum*, and *O. moubata*. These findings may suggest the possible presence of different species within these taxa or the existence of phylogeographical structure, wherein populations may originate from distinct geographic regions with limited or no gene flow.

Similar patterns have been documented in other taxa. For instance, Bergsten et al. (2012) demonstrated that increasing the geographic range of sampling can lead to an increase in genetic divergence (Bergsten et al., 2012), highlighting the influence of geographic structure on genetic divergence and species delimitation. Furthermore, while 16S rRNA is a useful marker for tick identification, it may not be sufficient as a single marker to resolve the specimens in question. Therefore, the incorporation of additional molecular markers such as COI and 12S rRNA could offer greater resolution.

5. Conclusion

Our study expands knowledge of tick species associated with African pangolins, including the first record of *Amblyomma compressum* on *Phataginus tetradactyla* and a newly recognized association between *Amblyomma hebraeum* and pangolins. *Rhipicephalus simus* and *Rhipicephalus theileri* were also identified, with the latter found exclusively on *Smutsia temminckii*. Genetic analyses confirmed the identity of most tick species, but *Ornithodoros compactus* showed high similarity to *Ornithodoros moubata*, indicating taxonomic challenges within the genus and warranting integration of other identification methods.

Given that some of these tick species are known vectors of pathogens affecting wildlife, livestock, and humans, our findings underscore the need for continued surveillance and monitoring of tick-borne diseases in confiscated scales and rehabilitated pangolins. Further research should investigate other molecular markers and the epidemiological implications of these tick-host associations, particularly in conservation and rehabilitation settings to better understand potential health risks and inform management strategies for pangolin conservation.

CRediT authorship contribution statement

Zwannda Nethavhani: Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Thando Radebe:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Catherine Maria Dzerfos:** Writing – review & editing, Methodology, Investigation. **Essa Suleman:** Writing – review & editing, Methodology, Investigation. **Raymond Jansen:** Writing – review & editing, Methodology, Investigation, Conceptualization.

Institutional review board statement

The animal study protocol was approved by the Ethics and Scientific Committee of the National Zoological Gardens (project P15/08), and The Department of Agriculture (Ref: 12/11/1/1/18), Forestry, and Fisheries, under Section of the Animal Diseases Act (Act No. 35 of 1984).

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Declaration of competing interests

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijppaw.2025.101117>.

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